A NEW ?BRYOZOAN FROM THE CARBONIFEROUS OF EASTERN AUSTRALIA

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ABSTRACT. Revision of Australian Carboniferous cryptostome fenestrate bryozoans has resulted in the recognition of a new genus, *Septatopora*, which has been defined on the basis of nine species, four of which, *S. flemingi*, *S. gloucesterensis*, *S. nodosa*, and *S.*(?) *williamsensis*, are new, with the remaining five species having been previously assigned to *Fenestella* Lonsdale or *Polypora* M'Coy.

The existence of eight apertural septa and an additional orifice on the branch surface proximal to each aperture, place the affinities of the genus in doubt. Grouping with either bryozoans or octocorals is suggested, with the conclusion being drawn that greatest affinities lie with the contemporary genera of fenestrate bryozoans. A new family, doubtfully positioned close to the Family Fenestellidae King, 1850, is erected to contain the new genus.

A BIOSTRATIGRAPHICAL, taxonomic, and evolutionary study of Australian Carboniferous fenestrate bryozoans, has led to the recognition of a new, morphologically distinct group of species, previously described members of which have been distributed generically between *Fenestella* Lonsdale and *Polypora* M'Coy.

Division of Australian species between these two taxa, based largely upon the number of rows of zooecial apertures per branch, has been found to be impractical. There exists a distinct evolutionary trend throughout the Carboniferous Period for all initially two-rowed fenestrate species to develop a third row of apertures at an increasing distance proximal to each branch bifurcation. One result of this is that it is no longer possible to decide if some Mid to Upper Carboniferous species are basically two- or three-rowed forms. This problem has already been raised in the case of *Fenestella*(?) *altinodosa* Campbell (Campbell 1961) where that author suggests his species could equally well be placed in *Polypora* M'Coy.

As a result of an extensive statistical survey in the present study of numerous Australian Carboniferous fenestrate specimens it became apparent that there were variations in apertural form, in conjunction with several other features, which provided a more satisfactory grouping of the Australian material. In particular, three basic types of aperture were recorded, namely:

1. Fenestellid type—a simple, weakly exserted, circular aperture with a narrow peristomal rim. Mean apertural diameter lies between 0·08 and 0·15 mm.
2. Polyporid type—a larger, simple aperture with a broad, low, peristomal collar which may become horseshoe-shaped in some species. Mean apertural diameter is usually about 0·14–0·23 mm.
3. Septate type—a circular, strongly exserted aperture with a thin, high peristome within which there are eight radially disposed septa surrounding a very small central orifice. Mean apertural diameter ranges between 0·07 and 0·13 mm.

This last group was also found to share several additional morphological features which together define the new genus described here as *Septatopora* gen. nov.

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The geological range of this new genus commences in strata which can be correlated, on the basis of other fauna, with the Tournaisian–Viséan boundary. It extends up through the remainder of the Australian Carboniferous sequence but has not yet been recorded from the overlying Permian strata. For purposes of brevity the following morphological discussion will refer to low, mid, and high zonal distribution, each of which correlates approximately with Lower Viséan, Upper Viséan–Namurian, and Westphalian–Stephanian respectively. More specific stratigraphic data are given with the systematic descriptions.

A total of nine species, two of which are of dubious relationship, are here assigned to the new genus:

Septatopora pustulosa (Crockford) 1949 [= *Polypora pustulosa*]
Septatopora flemingi sp. nov.
Septatopora isaacsensis (Campbell) 1961 [= *Polypora isaacsensis*]
Septatopora stellaris (Campbell) 1961 [= *Fenestella stellaris*]
Septatopora(?) *sulcifera* (Crockford) 1947 [= *Polypora sulcifera*]
Septatopora gloucesterensis sp. nov.
Septatopora acarinata (Crockford) 1947 [= *Fenestella acarinata*]
Septatopora nodosa sp. nov.
Septatopora(?) *williamsensis* sp. nov.

The stratigraphic distribution of these species is illustrated in text-fig. 2.

DIAGNOSTIC MORPHOLOGY OF *SEPTATOPORA*

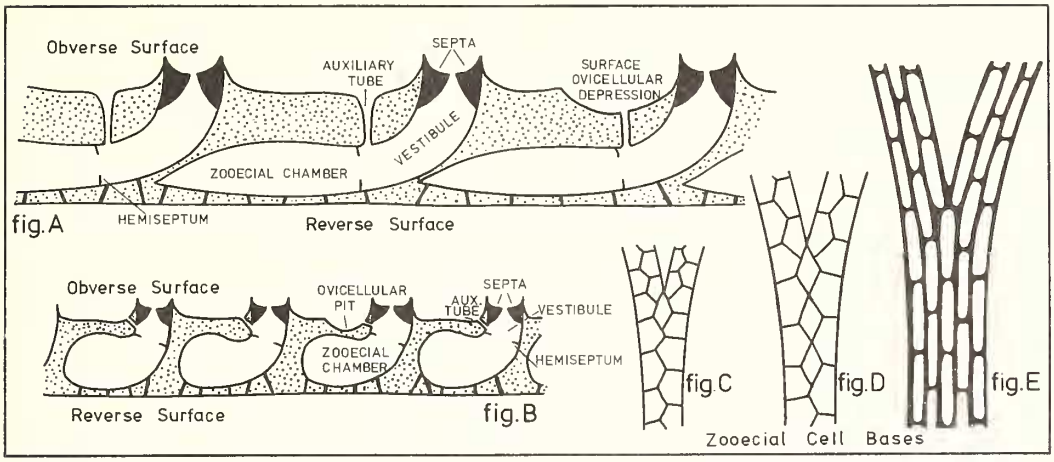
Apart from the fact that all species have a standard cryptostome fenestrate meshwork with a normal zooecial chamber/vestibule arrangement, the following are the four major, additional generically-distinguishing morphological features:

Septation. All apertures are strongly exserted and contain eight apertural septa which commence on the sides of the vestibule from where they taper upwards and inwards towards the axis to leave only a small circular opening in the centre of the external aperture. Each aperture also bears a narrow, elevated peristomal collar which gives it a cup-like form very similar to the calice of some solitary corals.

Auxiliary tube. In low zonal species the proximal side of the exserted aperture has a small opening or gap on to the obverse branch surface. This detail is quite difficult to observe in the very fine meshwork of these older species.

Upper zonal species have an obvious small, conical or slit-like depression situated some distance proximal to each aperture on the branch surface. This depression bears the surface ornament of the branch and is connected by a narrow auxiliary tube to the proximal region of the elongated vestibule just anterior to the hemiseptum. Position and orientation of the auxiliary tube vary according to the form of the zooecial chamber.

Ovicellular structures. Most species have additional large, irregularly spaced, hemispherical depressions on the branch surface. When present, they are situated adjacent to the proximal rim of an aperture where they obliterate the smaller conical depression. The surface of these larger depressions is smooth and they are also connected



TEXT-FIG. 1. A, B, side-sectional diagrams along one row of zooecial apertures in a branch showing zooecial chambers, hemisepta, septate vestibules, auxiliary tubes, and surface ovicellular depressions. (A, *Septatopora flemingi*, × 75; B, *Septatopora acarinata*, × 60.) C, D, E, reverse views of the method of packing of zooecial chambers immediately beneath the back wall of the branch. C illustrates a low zonal species with only one additional aperture appearing at bifurcation. D is a mid-zonal species with a third row of apertures appearing some distance before bifurcation. E demonstrates the change in zooecial packing in the late Carboniferous forms. (C, *Septatopora acarinata*, × 25; D, *Septatopora gloucesterensis*, × 25; E, *Septatopora flemingi*, × 20.)

to the lower vestibule by the auxiliary tube. They may be the sites of former external ovicellular chambers.

Ornamentation. Most species lack carina and are ornamented with fine, pustulose, sinuous, longitudinal striations of distinctive appearance.

The above features define a morphologically compact species group different from other fenestrate taxa. Several other variable features have proved also to be of considerable stratigraphic value. They are detailed in the comparative discussion which follows the description of each species.

SEPTATOPORA—BRYOZOAN OR OCTOCORAL?

The classification of *Septatopora* gen. nov. presents numerous difficulties which cannot be resolved on the basis of evidence at present available. The novel occurrence of eight septa in the vestibule of a form with a fenestrate bryozoan habit combines aspects of both bryozoan and possibly octocorallian affinities, a final decision between which must await further detailed thin section study.

Unfortunately, with rare exceptions, Eastern Australian Carboniferous fenestrate species are preserved in fine clastic sediments as either internal or external moulds, the original calcareous skeleton having been leached away or perhaps replaced by structureless secondary mineral deposition (calcite or hydrous silica). Consequently, almost no information is available on skeletal microstructure. Despite this serious deficiency, it is possible to reconstruct from the moulds many of the important structural details, some of which would be quite difficult to observe on complete specimens.

Amongst the rare material suitable for thin section work, all sections made so far have revealed a standard fenestellid microstructural arrangement (Tavener-Smith 1969; Tavener-Smith and Williams 1972). Unfortunately most of these sections have not been identifiable generically, and hence it is not possible to be certain that specimens of *Septatopora* have been included, although by their frequency, this is thought to be quite probable. Some internal moulds of *Septatopora* exhibit short skeletal rods which extend from the base of the zooecial chambers out to the side and reverse walls of the branch. These rods are almost certainly a replacement of the skeletal rods which occur normally in the laminated wall tissue of all fenestellids, lending further support to the supposition that the microstructure of *Septatopora* is of the fenestellid type.

Despite the major problems which will arise consequent upon the decision, the writer is of the opinion that *Septatopora* must be classified with its contemporary fenestellids. In recognition of its distinct morphology, the genus has been placed herein in a separate family and, with slight reservation, grouped most closely with the Family Fenestellidae pending the resolution of the generic microstructural details of the new genus. Some of the reasons for this decision are given below.

Growth habit. Where known, species of *Septatopora* have a broadly funnel-shaped or flared zoarium structurally identical with contemporary fenestellids. Apertures are arranged in regular rows along the branches on the inner surface of the cone. Exact equivalence of so many structural aspects is so great that an explanation of similarity based upon convergence from separate phyla is regarded as being highly improbable. Both *Fenestella*/*Polypora* and *Septatopora* also exhibit the same evolutionary trends throughout the Carboniferous in the development of their zoaria, some details of which are discussed later.

In Lower Carboniferous species septation is the major visible distinguishing feature, and in the case of poor preservation of this aspect, it is not possible to make a generic decision between *Septatopora* and *Fenestella*. It is only in the much larger, late Carboniferous species that the septation and auxiliary tube become readily evident, but even there the similarity of form is still very clear.

Growth habit in the octocorals is of extremely wide variation and a fenestrate form is known in a number of groups (e.g. gorgonids). No examples have been observed of the regular funnel-shaped zoarial form, and, although of limited significance, size differences between this group and *Septatopora* are of quite major proportions.

Septation. The existence of eight apertural septa is considered to be the main argument against a bryozoan origin for *Septatopora*. Modern ideas of the lophophore and gut of a bryozoan would appear to be incompatible with septation. It is not possible to argue this matter without further details of the skeletal microstructure of the vestibular region.

It should be pointed out that the septation is generally much shorter (longitudinally) than the vestibule in which it is housed and there appears to be no difficulty with the protrusion of the tentacles between the septa. In their fully extended mode, the tentacles would fill the calice-like external aperture and raise the mouth to a position beneath the central orifice in the base of the calice. To do this requires some slight invagination of the tentacle ring which in turn would provide a suitable secreting

surface for the septal development. Such possible modifications to the lophophore require further investigation.

An additional aspect of septation concerns the type species of *Polypora* M'Coy (*P. dendroides* M'Coy) which has been redescribed by Miller (1963) as having apertures with 'fifteen or sixteen short thin internal projections resembling the septa of corals'. Although of only slight form, their presence and number is highly suggestive, and lends some possible support to the argument that *Septatopora* should be grouped with these fenestrates.

Internal form. In spite of a lack of thin-section detail it is possible to establish that, internally, *Septatopora* is quite different from most octocorals of comparable arborescent form.

All species of *Septatopora* have a calcified skeleton in which the body chambers are regularly packed in contact with each other in rows adjacent to the thin reverse wall in a fashion identical with that of the fenestellids. These body chambers almost fill the branch having some variable skeletal thickening surrounding them.

In the space available in each branch it is quite impossible to develop an inner coenenchymal (medullar or axial) zone with an outer layer in which the chambers are shallowly embedded, as is a common condition in the gorgonid octocorals. It would appear that there is a variety of similar basic structural differences between *Septatopora* and most arborescent groups of living and fossil octocorals which would make their combination improbable.

Finally, all zooecia in *Septatopora* are distinctly subdivided into a body chamber and a vestibule separated by a marked hemiseptum. This dual chamber arrangement appears to have no modern analogue in the octocorals but is a well-established bryozoan feature.

Septation remains the most difficult aspect of the new genus to encompass within modern ideas on bryozoans. Despite this problem, the case has been argued above that *Septatopora* is basically inseparable from its contemporary fenestellids with which it closely approximates in both structure and form. It would seem that if *Septatopora* is unacceptable within the Phylum Bryozoa, then further close investigation must be made of the systematic position of the Family Fenestellidae.

FUNCTIONAL MORPHOLOGY

Whilst lacking any clear understanding of the reasons behind the development of apertural septation in all species of *Septatopora*, it is readily evident that the polypide was greatly restricted in its ability to extrude out of the zooecial cavity. In the fully extended mode, the tentacles would have been placed between the septal partitions and the mouth must have been located beneath the small central opening in the base of the calice-like depression. Of necessity, the tentacle ring or lophophore was thus contained within the vestibule. Assuming the genus was a normal ectoproct, this means that the anus, being outside the lophophore, would also have been enclosed within the vestibule. To overcome this major problem, the development of a separate anal opening would seem to have been an essential requirement.

In low zonal species with their globular zooecial chamber close to the obverse surface it is postulated that this was initially achieved by the simple development of

a breach in the side of the exserted vestibule, or by the construction of a short, narrow, horizontal connection from the base of the vestibule to the branch surface on the proximal side of the aperture. In high zonal species the chamber became elongate oval in form and located quite close to the reverse branch surface. This required the elongation of both the vestibule and the auxiliary 'anal' tube, each of which then developed as quite separate structures situated perpendicular to the branch surface. From the simple expedient solution of a lateral breach in the side of the exserted aperture, changes in chamber shape and position would thus have inevitably resulted in the need for the elaborate auxiliary tube as can be observed in the late Carboniferous representatives of the genus. It is perhaps not surprising that such a complex arrangement apparently did not survive beyond the Carboniferous Period.

It also appears reasonable to postulate that the reproductive system would have used this auxiliary tube for the release of fertilized ova which were then stored in enlarged spherical chambers on the branch surface, prior to final release. This would explain the coincidence of the auxiliary tube opening with the frequent, large hemispherical depressions observed on the branch surface adjacent to the proximal rim of selected fertile polypides in most zoaria.

The assignment of such an alimentary/reproductive role to the auxiliary tube presents several major difficulties. It is customary to extrapolate backwards from modern functional morphology to fossil morphology and unfortunately there appears to be no modern equivalent which can lead to the above interpretation. Modern calcified bryozoans have a budding pattern in which the anus is distally placed in the tentacular crown and given this information it is quite difficult with the budding pattern in *Septatopora* to postulate a proximal anus. Study of all species of *Septatopora* makes it quite evident that the auxiliary tube connects to the base of the vestibule adjacent to the hemiseptum making it obligatory to propose a proximal anus if the above proposed theory is to have any substance. In addition, modern species have their coelomic pores for egg extrusion placed distally and the transfer of eggs to the distally positioned brooding cavities requires a great deal of movement and manipulation on the part of the tentacle crown, a process clearly not possible from the base of the vestibule. Finally, external proximal ovicells are unknown in modern forms although little doubt is held that this is the only likely interpretation of these large, spherical, proximally situated structures in the fossil species.

From the above discussion it is apparent that an alimentary/reproductive role for the auxiliary tube requires a major reversal of the polypide construction from fossil to modern species. Although the proposition remains attractive, the absence of skeletal detail makes it impossible to arrive at a positive conclusion.

A second suggestion that the auxiliary tube served an hydrostatic function, with the surface opening being analogous to an ascopore is possible. This structure is defined by Bassler (1953) as a 'median small opening in the frontal wall of some cheilostomes leading to the compensatrix, located proximally with reference to the aperture'. There is a close similarity with this cheilostome feature and the opening found in *Septatopora* making it necessary to propose an hydrostatic function as an alternative explanation. However, since the polypide was unable to move very far because of the septation, it is unlikely to have developed the need for any great degree of compensation. The term 'ascopore' has been used for several non-homologous

systems in bryozoans and it is possible that other hydrostatic functions than that of compensation may have been the role of the auxiliary tube.

Although of major significance to the interpretation of the new genus, a lack of thin-section data and modern analogous structures means that a satisfactory explanation has yet to be achieved for the biological function of the apertural septation and its closely associated, proximally situated auxiliary tube.

Abbreviations. The following abbreviations are used in the statistical treatment of fenestrate mesh. FL = fenestrule length (centre to centre of dissepiments); FW = fenestrule width (centre to centre of branches); BW = branch width; DW = dissepiment width; ZD = zooecial diameter; Z-Z = zooecial aperture spacing (centre to centre of apertures); N-N = nodal spacing; F/10 = number of fenestrules in 10 mm; B/10 = number of branches in 10 mm; Z/5 = number of zooecial apertures in 5 mm; N/5 = number of nodes in 5 mm; Z/F = number of zooecial apertures per fenestrule; m = arithmetic mean value of dimension; s = standard deviation; OR = observed range of dimension; N = number of measurements recorded.

Repositories. All specimens have had their catalogue number prefixed by the letter 'F', preceded by the following Museum coding: QU = Queensland University; QGS = Queensland Geological Survey; NEU = University of New England; NU = University of Newcastle; SU = Sydney University.

Most specimens recorded by Crockford (1947, 1949) in the University of Queensland Catalogue have had new numbers allocated since their original publication.

Fossil localities. Localities are recorded, wherever possible, with the prefix NUL, followed by a number, all of which refers to the University of Newcastle Fossil Locality Index. Localities not present in that index are given in descriptive detail in the text. NUL9—3 km east of Booral, N.S.W. (Campbell 1961); NUL39—Cameron's Bridge, Rouchel Brook, N.S.W. (Crockford 1947); NUL258—Barrington, N.S.W. (Cvancara 1958); NUL361—Glen William, north of Clarencetown, N.S.W. (Crockford 1947); NUL372—Hilldale, N.S.W. (Crockford 1947); NUL390—Oaky Creek, N.S.W. (Campbell 1962); NUL414—Barrington Guest House, N.S.W. (Crockford 1947); NUL448—Raglan property, east of Dungog, N.S.W.; NUL454—Isaacs Road, Dungog 1 mile Military Map (Grid Reference 019840), N.S.W. (Campbell 1961); NUL472—Ridgelands 1 mile Military Map (Grid Reference 194827), Queensland (Fleming 1969).

Photographic methods. Because most specimens used in this study occur as external moulds, it was generally necessary for photographic purposes to prepare latex casts which were firstly painted with a uniform black coating over which a thin grey-white layer of ammonium chloride was deposited. Depending upon the size of the specimen and the magnification required, photographic negatives were produced with a stand-mounted, close-up camera, or with a camera attached to a stereobinocular microscope.

SYSTEMATIC DESCRIPTIONS

Phylum ?BRYOZOA
Order ?CRYPTOSTOMATA Shrubsole & Vine, 1882
Family SEPTATOPORIDAE fam. nov.

Type genus. Septatopora gen. nov.

Family diagnosis. ?Cryptostomata with zoaria of a broadly flared funnel shape with obverse surface on inner side of cone; composed of sub-parallel to radiating non-carinate branches connected by non-celluliferous dissepiments into a regular fenestrate meshwork; branches with two to four rows of small to medium-sized, strongly exserted calice-like apertures; apertures bear eight septa which taper upwards and inwards from the sides of the vestibule, converging in the base of the external aperture on a small central orifice; branch surface with fine pustulose, striate ornament; nodes present or absent, but when developed, irregularly placed on the distal rim of some

apertures; hemiseptum distinct; base of vestibule connected to branch surface where a second opening is located on the proximal side of each aperture.

Geological range. Upper Tournaisian to Stephanian.

Remarks. This family has been erected solely for the reception of the new genus *Septatopora* which cannot readily be combined with any other existing taxon. For reasons outlined in the previous discussion, the new family is regarded as belonging to the Order Cryptostomata Shrubsole & Vine, 1882, and is doubtfully grouped closest to the Family Fenestellidae King, 1850, with which it would appear to share the greatest number of common features.

Genus SEPTATOPORA gen. nov.

Type species. Septatopora pustulosa (Crockford) (= *Polypora pustulosa* Crockford, 1949).

Generic diagnosis. See family diagnosis given above.

Generic description. Septatoporid with zoaria of a flared funnel shape (where known) with obverse surface on inner side of cone; fine to medium-sized fenestrate mesh composed of narrow to wide, finely striated, pustulose branches, each having a rounded, non-carinate cross-section; fenestrules oval to sub-rectangular being moderately to strongly indented by zooecial apertures; apertures small to medium-sized, circular, septate, strongly exserted, being surrounded by a thin, high, complete peristome of calice-like form; apertures in two to four rows per branch with increase in number before, and decrease after, each branch bifurcation; nodes absent or irregularly developed adjacent to the distal or disto-central rim of some apertures in any zooecial row; arrangement may appear more regular in branches with only two rows of zooecia.

Zooecial chambers globular to elongate oval in form, being joined on their distal margin to curved or L-shaped vestibules respectively; distinct hemiseptum at base of vestibule; each vestibule with eight short, radially disposed septa extending upwards and inwards from the sides of the vestibule to converge on a narrow axial opening in the centre of the external aperture, which thus assumes a rosette pattern on the base and sides of the calice-like depression.

Additional small, funnel-shaped depressions located on the branch surface, proximal to each aperture; a narrow tube connects this orifice to the base of the vestibule just anterior to the hemiseptum; irregularly disposed, larger, smooth, hemispherical depressions may occur on the branch surface where they replace the funnel-shaped depressions and abut against the proximal rim of an aperture.

Reverse surface of rounded, pustulose branches joined by narrower, near level, sometimes inclined dissepiments; some reverse branches may also bear numerous, irregularly arranged spines. Zooecial bases irregularly pentagonal in lateral rows and rhomboidal in central rows; with increase in the number of zooecial rows they become elongate oval with little overlap between rows.

Geological range. Upper Tournaisian to Stephanian.

Generic comparisons. The reasons for excluding *Septatopora* from either *Fenestella*

Lonsdale or *Polypora* M'Coy have been discussed previously. No other genus of comparable form has been observed in the literature.

It is possible that the species discussed by Miller (1963) as *Polypora*(?) *verrucosa* (M'Coy) could be assigned to this genus. In his revision of *Polypora* M'Coy, Miller excluded this species on the basis of its stalk-like apertures, but was not prepared at that stage to designate a new generic category until similar morphology had been observed on further material. In its apertural form, the species is quite similar to *Septatopora*, but until further examination of the original material is made it is not possible to confirm its inclusion.

Septatopora pustulosa (Crockford), 1949

Plate 67, figs. 1–9

1949 *Polypora pustulosa* Crockford, p. 426, text-fig. 9.
1949 *Polypora tenuirama* Crockford, p. 428, text-fig. 11.
1961 *Polypora septata* Campbell, pp. 462–463, pl. 58, figs. 1–2.
1962 *Polypora* cf. *septata* Campbell, p. 47, pl. 13, fig. 8*a–c*.
1972 *Polypora pustulosa* Crockford; Fleming, pp. 6–7, pl. 3, fig. 8; pl. 4, figs. 1–6; text-figs. 1–2.

Revised diagnosis. Septatopora with wide pustulose branches; mesh open, medium-sized, with sub-oval to sub-rectangular fenestrules; apertures septate, strongly exserted, distantly spaced, with frequent, proximally associated, auxiliary pits and hemispherical depressions; zooecia in three rows per branch; carina and nodes lacking; reverse branch profile rounded; zooecial bases elongate oval.

Revised description. Zoarium: gently radiating to sub-parallel branches of maximum radius 90 mm; orientation unknown. *Obverse surface.* (*a*) *Branches.* Wide, normally with three rows of zooecia (m.BW 0·49 mm); two-rowed branches medium to narrow (~0·3 mm) and four- to five-rowed branches very wide (~0·8 mm); branch cross-section rounded, becoming oval at bifurcations; ornament of distinctive pustules arranged along slightly wavy, faint, longitudinal ribbing. (*b*) *Dissepiments.* Medium to wide (m.DW 0·21 mm); expanded gently outwards from centre to branch junction in a broad curve; level with or slightly below branches; most dissepiments inclined towards base of colony; ornament as on branches. (*c*) *Fenestrules.* Sub-oval to sub-rectangular; medium-sized mesh moderately regular but varied by regions of wide pre-bifurcation, and narrow post-bifurcation branches; fenestrules wider than branches, resulting in an open-mesh appearance; fenestrules medium length (m.FL 1·68 mm), medium to wide (m.FW 1·03 mm). (*d*) *Carina.* Absent. (*e*) *Nodes.* Absent. (*f*) *Zooecial apertures.* Medium size, circular (m.ZD 0·11 mm); strongly exserted being surrounded by high peristome; apertures bear eight radially disposed septa surrounding a narrow axial opening which widens downwards towards the zooecial chamber; erect or laterally inclined apertures arranged in straight rows with alternating positions in adjoining rows; marginal apertures strongly indent fenestrules and are not stabilized with respect to the dissepiments; apertures in each row medium to distantly spaced (m.Z–Z 0·43 mm) with from three to five zooecia per fenestrule (m.Z/F 3·9); usually three rows per branch with increase to four (rarely five) rows up to 2 mm before, and decrease to two rows up to 2 mm after bifurcation. (*g*) *Additional features.* Proximal to each aperture there is a small, funnel-shaped pit which

bears normal, slightly deflected branch ornament; a narrow tube connects the bottom of this pit to the base of the vestibule; some specimens also bear irregularly distributed, smooth, hemispherical depressions (diam. 0·25–0·35 mm) on the obverse branch surface, situated so that the distal rim of the depression is in contact with the proximal margin of an aperture; an opening at the base of the depression may be visible, being the site of the tubular connection.

Reverse surface. (*a*) *Form.* Broadly rounded branches joined by medium width, level dissepiments; both branches and dissepiments bear fine, pustulose striations. (*b*) *Zooecial bases.* Elongate oval with little or no overlap between adjoining rows of zooecia.

Material. Holotype QUF24980; topotype QGSF10910 (Por. 2v. Ph. Stanwell); others QGSF11920, QGSF10936 (Neerkol Creek); QGSF10905, QGSF10988–10989, QGSF10889 (Malchi Creek); QUF24954–24955 (Malchi Creek); NEUF4708D, NEUF4715C/D, NEUF4734C/D (NUL9); NEUF5632–5634 (NUL390). Further material from various localities in New South Wales and Queensland has been placed in the University of Newcastle Collection.

Remarks. Fleming (1972) first proposed that the three species *P. pustulosa* Crockford, *P. tenuirama* Crockford, and *P. septata* Campbell should be combined into the one species. Concurrent and subsequent detailed mesh studies by the present writer strongly support this decision. However, the work of Miller (1963) clearly indicates that the Australian material cannot be assigned to the genus *Polypora* M'Coy, and hence a new genus is proposed here for its reception.

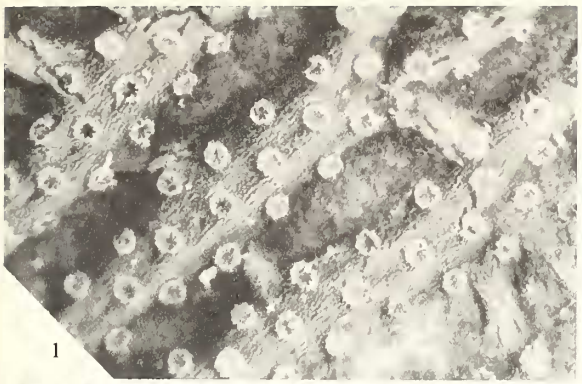
Based upon Queensland specimens, Crockford (1949) erected both her species in the one paper, but made no comparative remarks. Distinction appears to have been based upon absolute differences in mesh size and zooecial spacing. No mention was made of apertural septation in *P. pustulosa*, no doubt because of the very poor state of preservation of the type material.

Campbell (1961) erected the third species *P. septata* upon specimens from New South Wales, and hesitantly distinguished it from *P. tenuirama* because of small differences in mesh dimensions and apertural septation. Further specimens from another New South Wales locality (Campbell 1962) were referred to *P.* cf. *septata* because of their weak development of apertural septation, a reduced branching frequency, an

EXPLANATION OF PLATE 67

All figures of latex casts except fig. 7.

Figs. 1–9. *Septatopora pustulosa* (Crockford). 1–4, obverse surface of holotype of *Polypora septata* Campbell, NEUF4708D, ×20, ×30, ×30, ×50 respectively. Note auxiliary openings proximal to each aperture on figs. 1 and 2 and strongly exserted, septate form of apertures together with the distinctive pustulose ornament on branch surfaces in figs. 3 and 4. 5, 6, obverse surface of holotype of *Polypora tenuirama* Crockford, QUF24955, ×20, ×10 respectively. Note frequent occurrence of proximal ovicellular pits. Weaker occurrence of surface ornament is due to preservation. 7, reverse view of zooecial chamber infillings of *P. tenuirama* Crockford showing skeletal rods extending between chamber and walls, QUF24955, ×5. 8, obverse surface of QGSF10988, ×5. 9, obverse surface of QGSF11920, ×5. (Figs. 1–4 from locality NUL9, Booral, N.S.W.; figs. 5–9 from Malchi Creek, Queensland.)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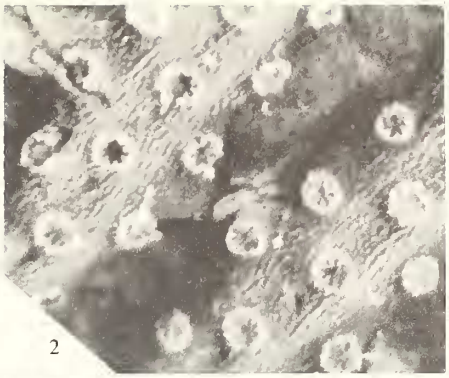
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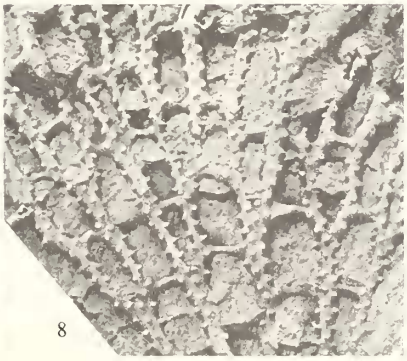
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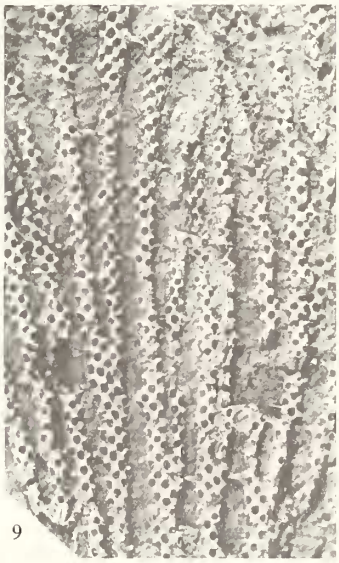
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ENGEL, *Septatopora*

increase to five, rather than four zooecial rows before bifurcation, and the development of surface hemispherical depressions not previously observed on *P. septata*.

Detailed measurement by the present writer on a wide variety of specimens from both states, including all type material, has established that all three species belong to the one continuously expanding mesh series, and that there are no grounds for subdivision upon this basis. Furthermore, all material bears the diagnostic obverse features of pustulose ornament, apertural septation, and separate auxiliary orifices, and is therefore considered to be conspecific.

All authors have recorded the occurrence of surface hemispherical depressions (?ovicell sites) but Fleming (1972) also noted a few of the smaller openings on one specimen (holotype of *P. tenuirama*) and described them as incompletely formed ovicellular structures. Close examination of most specimens reveals this structure to be associated with all apertures as a basic functional feature.

Septatopora pustulosa (Crockford) has been chosen as the type species of the new genus because of its widespread, common occurrence in Eastern Australia. Further, it is generally of sufficiently coarse mesh to enable easy recognition of the diagnostic features of the genus.

Stratigraphy. S. pustulosa (Crockford) has a wide geographic and stratigraphic range through the *Levipustula levis* Zone in Australian Upper Carboniferous sediments. It is found intermittently through the whole thickness of the Neerkol Formation (2100 m) near Rockhampton, and in the Poperima/Rands Formations (Maxwell 1964) in the Yarrol Syncline of Queensland. Occurrences in New South Wales are more restricted but are found at various uncorrelated levels in the Booral Formation (2000 m) and in the Kullatine Formation as recorded by Campbell (1962).

The age of the *L. levis* Zone is generally considered to be Westphalian but no evidence exists for more precise correlation.

Septatopora flemingi sp. nov.

Plate 68, figs. 4–8; text-fig. 1A, E

Diagnosis. Septatopora with very wide, weakly pustulose branches; mesh closed,

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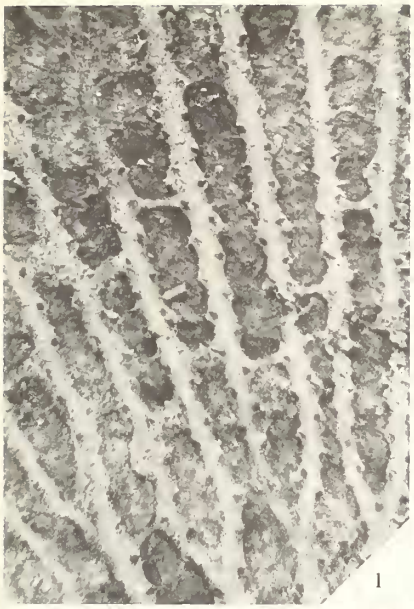
EXPLANATION OF PLATE 68

All figures of latex casts except figs. 6–8.

Figs. 1–3. *Septatopora*(?) *williamsensis* sp. nov. 1, 2, obverse surface of holotype showing lateral position of partly exserted apertures and the wide expanse in centre of branch without carina or nodes, NUF2421a, locality NUL414, ×10, ×30 respectively. 3, reverse surface of holotype, NUF2421b, ×10.

Figs. 4–8. *Septatopora flemingi* sp. nov. 4, obverse surface of holotype showing weakly exserted apertures together with their prominent adjacent auxiliary openings which form a longitudinal furrow between apertures in each row, NUF2357, locality NUL472, ×10. 5, obverse surface of NUF2362a, locality NUL472, ×5. 6, 7, oblique reverse view of an eroded zoarium with reverse wall removed. Visible is a complete internal mould of one chamber. In fig. 7 the upper vestibule is partly obscured by fenestrule infilling and only the curved and lower horizontal portion can be seen leading back to the distinct hemiseptum. Immediately below the hemiseptum, the vertical auxiliary tube (shaded) connects the lower vestibule to the obverse surface below. The body chamber extends to the right of the vestibule where its termination tends to merge with adjacent infillings, NUF2358, locality NUL472, ×20, ×40 respectively. 8, vertical view of same showing one complete chamber infilling from the reverse with adjacent infillings being broken off to leave the septate moulds of the upper vestibules, NUF2358, ×40.



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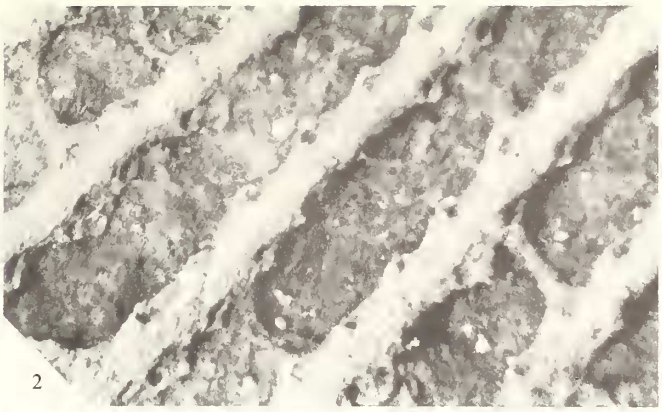

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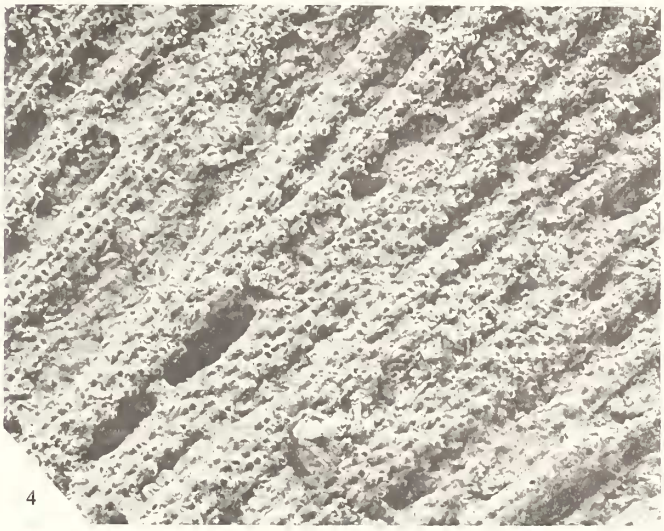

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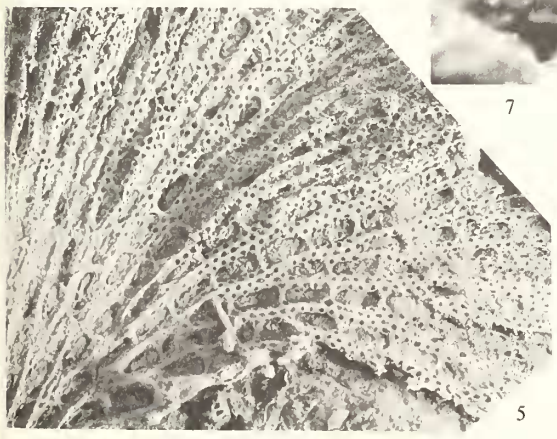

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ENGEL, *Septatopora*

medium-sized with sub-oval to sub-rectangular fenestrules; apertures septate, moderately to weakly exserted, distantly spaced with very strong development of proximal auxiliary pits; hemispherical surface depressions rare; zooecia in three or four rows per branch; carina and nodes absent, but with pseudo-carinal relief between zooecial rows; reverse branch profile rounded; zooecial bases elongate oval.

Description. Zoarium: moderately radiating to sub-parallel branches of maximum radius 40 mm; zoarial margins crenulate; orientation unknown. *Obverse surface.* (*a*) *Branches.* Wide to very wide (m.BW 0·54 mm), straight, usually with three to four rows of zooecia; branch cross-section round to oval, well-preserved branches bear sinuous, faintly pustulose, longitudinal ribbing of moderate elevation; large auxiliary orifices in the form of strongly depressed elongated pits extend between adjacent apertures; each apertural row appears to be located in a linear furrow and separated from adjoining rows by a weak carinal rise. This relief effect is more apparent on deflated branch surfaces. (*b*) *Dissepiments.* Medium to wide (m.DW 0·3 mm) with gradual expansion to branch junction in a gentle curve; level with or below branches, they are inclined with the obverse face being directed proximally; ornament as on branches. (*c*) *Fenestrules.* Sub-oval to sub-rectangular; mesh medium-sized, generally regular except in regions where several adjacent branches bifurcate; fenestrule openings narrower than branches resulting in a closed-mesh appearance; fenestrules of medium length (m.FL 1·65 mm) and medium width (m.FW 0·91 mm). (*d*) *Carina.* Absent. (*e*) *Nodes.* Absent. (*f*) *Zooecial apertures.* Medium size, circular (m.ZD 0·13 mm) moderately exserted being surrounded by an entire, low peristome; each aperture bears eight septa which taper down the sides of the vestibule; apertures are erect or laterally inclined, and arranged in three to four rows per branch with increase to five (rarely six) pre-bifurcation, and decrease to three (rarely two) post-bifurcation; apertures alternate in adjacent rows only slightly indenting the fenestrule margin and are not stabilized with respect to the dissepiments; spacing between apertures medium to distant (m.Z–Z 0·38 mm) with from three to five zooecia per fenestrule (m.Z/F 4·3). (*g*) *Additional features.* Elongate, proximally directed oval-shaped zooecial chambers are located close to the reverse surface wall. The long vestibule is geniculate in form with a short horizontal section being joined by a longer vertical section. Septa commence above the geniculation, and taper upwards and inwards towards the axis. The auxiliary tube extends vertically from the horizontal section of the vestibule immediately anterior to the strong hemiseptum, to join the branch in a deeply depressed slit-like surface pit of dimensions comparable with those of the adjacent aperture. Only rare hemispherical surface pits have been observed.

Reverse surface. (*a*) *Form.* Branches broadly rounded joined by medium width, near level or slightly depressed dissepiments both of which generally lack much ornament; some specimens bear strong, ribbed attachment spines. (*b*) *Zooecial bases.* Narrow, elongate oval in form, with little or no overlap between adjacent rows.

Material. Holotype NUF2357 (NUL472); paratypes NUF2358, 2360a/b, 2361, 2362a/b, 2365, 2366 (NUL472); others NUF2359a/b, 2363, 2364 (NUL472).

Remarks. Although quite similar to *S. pustulosa* in most mesh dimensions these

specimens display sufficient morphological differences to justify the erection of a new species.

Major differences between the two species are that *S. flemingi* has (*a*) an extra row of zooecial apertures in only slightly wider branches. Zooecia are more closely packed and apertures can be located low on the sides of the branches; (*b*) apertures which are somewhat larger but more closely spaced, and less exserted, resulting in reduced fenestrule indentation; (*c*) auxiliary tube openings very strongly developed being sub-equal to the apertures in size. This results in a crowded branch surface of distinctly different aspect to *S. pustulosa* where the auxiliary tube openings are still quite small. The strong depression of the auxiliary tube openings between apertures in *S. flemingi* results in linear furrows along the zooecial rows not seen in the other species. The opposed relief effect of apparent carinae between zooecial rows is another feature not observed on *S. pustulosa*.

Stratigraphy. S. flemingi sp. nov. is known only from the top 300 m of the Neerkol Formation as recorded by Fleming (1969) in association with the *Cancrinella levis* Zone. Because of lack of stratigraphic continuity it is not possible to be certain of the exact age of this late Carboniferous zone. However, the occurrence of an associated brachiopod–bivalve fauna of late Carboniferous–early Permian aspect would suggest that the *C. levis* Zone is at least of late Westphalian to Stephanian age.

The zone is known only from localities in the Stanwell–Ridgelands and Yarrol districts of Queensland.

Septatopora isaacsensis (Campbell), 1961

Plate 69, figs. 7–8

1961 *Polypora isaacsensis* Campbell, pp. 463–464, pl. 63, fig. 1*a–e*.

Revised diagnosis. Septatopora with wide, weakly pustulose branches; mesh closed, medium to fine with oval to sub-oval fenestrules; apertures septate, moderately exserted, medium spaced with frequent, proximally associated, hemispherical depressions obliterating most auxiliary pits; zooecia in three rows per branch; carina absent; blunt nodes distantly spaced; reverse branch profile tapered, with ornament of numerous irregular spines; zooecial bases oval.

Revised description. Zoarium: large zoarium of gently radiating, strongly crenulate branches; maximum radius of specimen 50 mm; obverse surface faces upwards on the interior of a broadly flattened cone-like zoarium. *Obverse surface.* (*a*) *Branches.* Wide (m.BW 0·47 mm), straight, broadly rounded to flattened with weak pustulose ornament. (*b*) *Dissepiments.* Medium to wide (m.DW 0·26 mm); growth expands from centre to branch junction in a semi-circular curve; level with, or just below, branches; no ornament observed. (*c*) *Fenestrules.* Oval to sub-oval; medium to small, moderately regular mesh with small fenestrule openings resulting in a closed appearance; short to medium length, medium width fenestrules (m.FL 0·91 mm; m.FW 0·75 mm). (*d*) *Carina.* Absent. (*e*) *Nodes.* Medium size, circular, blunt nodes very poorly developed due to large number of hemispherical depressions present; irregularly spaced when present (m.N–N 0·94 mm); usually located on distal rim of an aperture. (*f*) *Zooecial apertures.* Medium size, circular to slightly oval (m.ZD

0·12 mm); exserted with distinct peristome; eight septa in each aperture with a relatively large central opening; apertures erect, with slight fenestrule indentation, not stabilized with respect to dissepiments; apertures in each row of medium spacing (m.Z–Z 0·32 mm) with two to three zooecia per fenestrule (m.Z/F 2·8); three rows per branch increasing up to five pre-bifurcation. (*g*) *Additional features.* Obverse surface largely covered with many hemispherical depressions (diam. 0·2–0·25 mm) although smaller auxiliary tube pits can be observed at a few locations.

Reverse surface. (*a*) *Form.* Branches tapered becoming narrowly rounded and subequal to near level dissepiments; ornament of strong, variable-size spines arranged irregularly near the centre line of the branch. (*b*) *Zooecial bases.* Form not clear but have a well-rounded to oval form near the basal plate.

Material. Holotype NEUF4744A/C (NUL454).

Remarks. This species is known only by the holotype. No further material from the type locality has been found.

S. isaacsensis (Campbell) is the smallest Upper Carboniferous member of the new genus and can be grouped with *S. stellaris* (Campbell) and *S. gloucesterensis* sp. nov. on the basis of their common development of strong obverse nodes.

Stratigraphy. S. isaacsensis (Campbell) occurs only at one locality in the Isaacs Formation as described by Campbell (1961). By its association with rare specimens of *Levipustula levis* it is considered to be situated high in that zone, but unfortunately there are no overlying marine faunas at this locality which can be used to fix its position with any degree of accuracy.

The brachiopod fauna, with which *S. isaacsensis* is associated, is located about 1500 m above the profuse but vertically restricted development of the *L. levis* fauna near the base of the Booral Formation. On rather tenuous grounds therefore, the fenestrate species is considered to be of late Westphalian age.

Septatopora stellaris (Campbell), 1961

Plate 69, figs. 2–4

1961 *Fenestella stellaris* Campbell, pp. 456–457, pl. 58, fig. 4*a–d.*

Revised diagnosis. Septatopora with medium width, finely pustulose branches; mesh uniform, medium to fine, with oval to sub-oval fenestrules; apertures septate, strongly

EXPLANATION OF PLATE 69

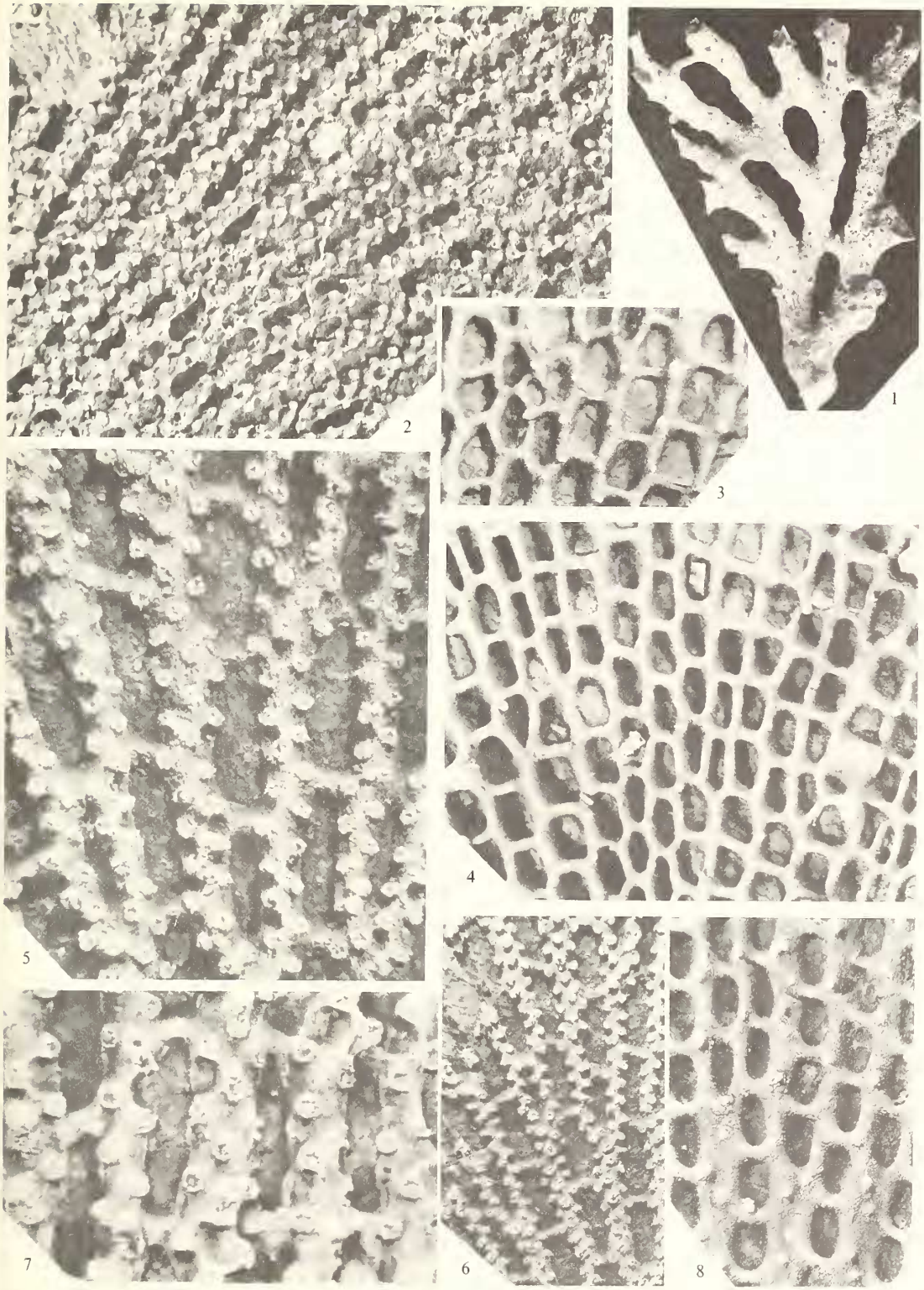
All figures of latex casts except fig. 1.

Fig. 1. *Septatopora*(?) *sulcifera* (Crockford). Obverse surface of holotype, QUF14909, locality Por. 21/22, Ph. Malmoe, Queensland, × 10.

Figs. 2–4. *Septatopora stellaris* (Campbell). 2, obverse surface of holotype, NEUF4716A, locality NUL9, × 10. 3, 4, reverse surface of holotype showing tapered branches with equal width to that of the dissepiments in a polygonal mesh. Note reverse surface spines, × 10, × 10 respectively.

Figs. 5–6. *Septatopora gloucesterensis* sp. nov. 5, 6, obverse surface of holotype, NUF2398, locality NUL258, × 20, × 10 respectively.

Figs. 7–8. *Septatopora isaacsensis* (Campbell). 7, 8, obverse and reverse of holotype, NEUF4744A/B, locality NUL9, × 30, × 10 respectively.



ENGEL, *Septatopora*

exserted, medium spaced, being associated with profuse, proximal, hemispherical depressions; zooecia in two to three rows per branch; carina absent; nodes large, irregular, distantly spaced; reverse branch profile tapered, with ornament of irregular spines; zooecial bases unknown.

Revised description. Zoarium: flattened, funnel-shaped expansion with a very small cone of attachment; maximum radius 55 mm; obverse surface faces upwards or to the interior of the funnel. *Obverse surface.* (*a*) *Branches.* Medium width (m.BW 0·36 mm), straight, broadly rounded with some deflation; ornament of fine ribbing and faint pustules. (*b*) *Dissepiments.* Medium width (m.DW 0·14 mm); growth expands from centre to branch junction in a semi-circular curve; level with branches; ornament of fine ribbing. (*c*) *Fenestrules.* Sub-oval to oval; medium to fine mesh; regular distally but variable proximally; fenestrule openings of about branch width resulting in a uniform appearance; short to medium length, medium width fenestrules (m.FL 0·95 mm; m.FW 0·63 mm). (*d*) *Carina.* Absent. (*e*) *Nodes.* Large, circular (diam. 0·15 mm), erect or slightly inclined distally; spacing irregular (m.N–N 0·95 mm) where present, but large areas nodeless; situated distal to an aperture resulting in zigzag placement on two-rowed branches but centrally placed in three-rowed branches. (*f*) *Zooecial apertures.* Medium size, circular (m.ZD 0·13 mm); strongly exserted with high peristome; each aperture with eight septa and strong axial tube; erect apertures moderately indent the fenestrules and are not stabilized with respect to the dissepiments; medium spacing (m.Z–Z 0·33 mm) with from two to three zooecia per fenestrule (m.Z/F 2·9); two rows of zooecia per branch with three rows developing up to half-way between successive bifurcations, but normally only for about one-third of this distance. (*g*) *Additional features.* Obverse surface covered by profuse hemispherical depressions (diam. 0·2–0·28 mm) situated between apertures and projecting into the fenestrule margin.

Reverse surface. (*a*) *Form.* Branches taper in width to become acutely rounded and equal in dimension to the near level dissepiments. Reduced branch width is accompanied by a wavy to zigzag branch outline which results in an irregular mesh of rectangular-polygonal fenestrules with no thickening at branch-dissepiment junctions; branch and dissepiment width about 0·2 mm; ornament of fine, longitudinal ribbing with a pustulose overgrowth; numerous irregularly disposed spines occur with large variation in size, position, and attitude; most are distally inclined. (*b*) *Zooecial bases.* Poorly preserved in type material, being of oval form some little distance above the basal plate.

Material. Holotype NEUF4716A/B (NUL9); paratype NEUF4717 (NUL9). Additional material in the University of Newcastle Collection.

Remarks. Campbell (1961) noted the very different morphology of this species as compared with other Carboniferous fenestellids, but was guided by the widespread development of two rows of apertures into placing it in the genus *Fenestella* Lonsdale. It is removed here from that genus on the basis of its distinctive apertural features.

There is a considerable degree of similarity between *S. isaacsensis* (Campbell) and *S. stellaris* (Campbell), but they can be readily distinguished by the number of rows

of zooecial apertures per branch at which taxonomic level this feature is given its greatest significance.

Stratigraphy. This species comes from low in the Booral Formation, where it is associated with the principal occurrence of *Levipustula levis.* To date it has only been found at localities of similar age in the Stroud–Gloucester Syncline, N.S.W. On this basis it can only be assigned a probable early Westphalian age.

Septatopora(?) *sulcifera* (Crockford), 1947

Plate 69, fig. 1

1947 *Polypora sulcifera* Crockford, pp. 15–16, pl. 1, fig. 2; text-fig. 13.

Revised diagnosis. Septatopora-like species with medium to wide, pustulose branches; mesh open, medium sized, with oval to sub-rectangular fenestrules; apertures small, strongly exserted, closely spaced, without visible septation; carina and nodes absent; reverse branch profile rounded; zooecial bases unknown.

Revised description. Zoarium: small fragment of radiating branches from base of the zoarium; orientation unknown; maximum radius 6·5 mm. *Obverse surface*: (*a*) *Branches.* Medium to wide (m.BW 0·41 mm), straight, slightly flattened (depth 0·36 mm); ornament of fine, pustulose ribbing. (*b*) *Dissepiments.* Small to medium width (m.DW 0·2 mm); centrally straight with slight expansion at branch junction; slightly depressed below branch level; pustulose ornament. (*c*) *Fenestrules.* Elongate oval proximally becoming sub-rectangular distally; proximal mesh, medium size, irregular with an open appearance; fenestrules of medium length and width (m.FL 1·36 mm; m.FW 0·74 mm). (*d*) *Carina.* Absent. (*e*) *Nodes.* Absent. (*f*) *Zooecial apertures.* Small (m.ZD 0·07 mm); circular; strongly exserted; no internal structure preserved; narrow peristome; apertures closely spaced (m.Z–Z 0·29 mm) with from three to six zooecia per fenestrule (m.Z/F 4·7) but distal portions indicate a distribution of five to six per fenestrule; three rows per branch with two or three post-bifurcation and three to five pre-bifurcation.

Reverse surface. (*a*) *Form.* Rounded branches joined by narrow, near level dissepiments, both of which bear pustulose ornament. (*b*) *Zooecial bases.* Unknown.

Material. Holotype QUF14908 (formerly QUF5768c) Riverleigh Limestone Por. 21/22, Ph. Malmoe, 8 km NW. of Mundubbera, Queensland.

Remarks. The only known specimen is the holotype which comprises two small, silicified fragments dissolved from the Riverleigh Limestone near Mundubbera, Queensland. Both fragments are very close to the base of the zoarium indicating little significance for the accompanying dimensions. Despite further solution of limestone no other samples have been recovered from the type locality.

Since morphological details of apertural structures, zooecial bases, and distal zoarial form are unknown, generic assignment must be conjectural. Based upon the occurrence of small, strongly exserted apertures on nodeless branches which bear only a fine ornament of pustulose striations, this species has been provisionally grouped with *Septatopora.* This assignment is subject to confirmation by the recovery of distally located, better-preserved specimens.

Stratigraphy. The Riverleigh Limestone, located in an isolated fault block, has been previously correlated with beds which lie just below the *Rhipidomella fortimuscula* Zone (Hill 1934; Driscoll 1960). More recent studies by McKellar (1967) and Jull (1968, 1969) indicate an older age which would correlate either with the *Delepinea aspinosa* Zone, or perhaps with the *Orthotetes australis* Zone. Experience in New South Wales would indicate this latter age is too old, since extensive sampling has failed to reveal any multi-rowed fenestrates in beds belonging to that zone. For the present, a *D. aspinosa* age is preferred, but no conclusive evidence for this age exists.

Septatopora gloucesterensis sp. nov.

Plate 69, figs. 5–6; text-fig. 1D

Diagnosis. *Septatopora* with medium width, weakly pustulose branches; mesh open, fine, with sub-oval to sub-rectangular fenestrules; apertures small, septate, strongly exserted, associated with numerous proximal, hemispherical depressions; zooecia in two to three rows per branch; carina absent; nodes small, irregularly placed, moderately spaced, situated on disto-central rim of some apertures; reverse branch profile rounded; zooecial bases irregularly pentagonal and rhomboidal.

Description. *Zoarium*: shallow, cone-shaped zoarium of radiating branches; obverse surface on interior of cone; maximum radius 20 mm. *Obverse surface*: (*a*) *Branches*. Straight, narrow to medium width (m.BW 0·3 mm); obverse acutely rounded with prominent apertures; ornament of fine pustules and very weak longitudinal ribbing. (*b*) *Dissepiments*. Medium to wide (m.DW 0·18 mm); centrally straight with moderate expansion to branch junction; profile tapers obversely so as to appear slightly carinate. (*c*) *Fenestrules*. Fine, slightly irregular, open mesh of sub-oval to sub-rectangular, medium to short length, narrow fenestrules (m.FL 1·12 mm; m.FW 0·58 mm). (*d*) *Carina*. Absent. (*e*) *Nodes*. Small, erect, irregularly developed, moderately spaced nodes (m.N–N 0·51 mm) situated adjacent to an aperture on its distal or central rim; most nodes placed near to centre of branch when present. (*f*) *Zooecial apertures*. Small, circular (m.ZD 0·1 mm); strongly exserted; narrow, entire peristome; apertures bear eight septa which radiate from a central perforation; erect apertures arranged in straight rows with moderate fenestrule indentation; mostly stabilized with respect to the dissepiments, on to which they commonly encroach; zooecia closely spaced (m.Z–Z 0·27 mm) with from four to five zooecia per fenestrule (m.Z/F 4·1); usually two to three rows per branch with increase to four rows up to 3 mm before bifurcation. (*g*) *Additional features*. Hemispherical depressions developed on branch surface between apertures and projecting into fenestrules; auxiliary tube connection to vestibule visible at base of depression; pronounced hemiseptum developed in most zooecial chambers.

Reverse surface. (*a*) *Form*. Rounded branches joined by slightly narrower dissepiments near branch level; ornament of fine pustules over longitudinal striations. (*b*) *Zooecial bases*. Elongate, irregularly pentagonal in two-rowed branches, becoming shorter where three or four rows occur; central rows rhomboidal in shape.

Material. Holotype NUF2398 (NUL258); paratypes NUF2383 (NUL258), NUF2425 (NUL414).

Remarks. This new species has the distinctive apertural features of the genus *Septatopora*. Further, it has considerable, more or less equal, areas of either two or three rows of apertures per branch, making it transitional from the older two-rowed species to the younger three-rowed forms. The existence of occasional nodes in a near central row is a further characteristic of this species.

Stratigraphy. S. gloucesterensis occurs in the *Delepinea aspinosa* and *Rhipidomella fortimuscula* Zones in New South Wales. As such it is the first occurrence of a multi-rowed fenestrate in the Australian Carboniferous sequence, and it is joined in the *R. fortimuscula* Zone by the first representative of the genus *Polypora* M'Coy. The incoming of these multi-rowed fenestrates is thus considerably younger than their development in other parts of the world, but their appearance in the Australian record is of maximum zonal value.

Septatopora acarinata (Crockford), 1947

Plate 70, figs. 6–8; text-fig. 1B, C

1947 *Fenestrellina acarinata* Crockford, p. 36, pl. 4, fig. 3; text-fig. 45.
1968 *Levifenestella acarinata* (Crockford) Wass, p. 87.

Revised diagnosis. Septatopora with narrow, straight to zigzag, pustulose branches; mesh open, fine, with sub-oval to sub-rectangular fenestrules; apertures small, septate, closely spaced, strongly exserted with frequent, proximally associated hemispherical depressions; zooecia in two rows per branch; carina and nodes absent; reverse branch profile rounded; zooecial bases irregularly pentagonal.

Revised description. Zoarium: shallow, cone-shaped zoarium of radiating branches; obverse surface on interior of cone; maximum radius 20 mm (holotype 6 mm). *Obverse surface.* (*a*) *Branches.* Narrow, straight or slightly zigzag; rounded profile without carina; ornament of very fine, pustulose, longitudinal striations (m.BW 0·21 mm). (*b*) *Dissepiments.* Medium width centrally with gradual expansion to branch junction in an expanding curve; some dissepiments inclined from vertical plane; level with or slightly below branches; ornament of fine striations (m.DW 0·11 mm). (*c*) *Fenestrules.* Fine, irregular mesh of sub-oval to sub-rectangular short, narrow fenestrules (m.FL 0·75 mm; m.FW 0·48 mm). (*d*) *Carina.* Absent. (*e*) *Nodes.* Absent. (*f*) *Zooecial apertures.* Small, circular (m.ZD 0·08 mm); strongly exserted; narrow, raised, entire peristome; apertures bear eight septa radiating from a minute axial tube; mostly erect with some lateral apertures moderately indenting the fenestrule margin; apertures generally stabilized with respect to dissepiments on to which they commonly encroach; zooecia closely spaced (m.Z–Z 0·25 mm) in each row, with from three to four zooecia per fenestrule (m.Z/F 3·0); two rows per branch with a third row appearing at or immediately prior to branch bifurcation. (*g*) *Additional features.* Large, hemispherical branch depressions located adjacent to the proximal rim of some apertures; horizontal lateral connection between exserted portion of vestibule and proximal branch surface occurs with all apertures; distinct hemiseptum visible on casts of most zooecial chambers.

Reverse surface. (*a*) *Form.* Branches and dissepiments rounded with the latter depressed

slightly below branch level; reverse wall very thin; ornament of longitudinal striations. (*b*) *Zooecial bases.* Irregularly pentagonal.

Material. Holotype SUF7402 (NUL372); paratypes SUF7406 (NUL372); SUF6438 (NUL361); others NUF2478, NUF2483–2485 (NUL448); NUF2518–2521 (NUL39); NUF2402–2403 (NUL414).

Remarks. S. acarinata (Crockford) has long been known as an aberrant species of *Fenestella* in that it lacks the generically diagnostic, nodose carina and has septate apertures. Wass (1968) placed the species in *Levifenestella* Miller, but this seems inappropriate, in view of the importance of the nodeless carina of that genus.

As at present defined, *S. acarinata* extends over a wide range covering much of the Viséan interval. It should be noted that the specimens from the lowest zone have a much narrower branch profile which appears to zigzag between apertures which thus dominate the obverse surface. By contrast, specimens from later zones have a more robust, rounded branch profile on which the apertures appear to have been superimposed. This variation in branch width has not been given taxonomic status at this time, although it results in specimens with quite dissimilar appearance.

Because *S. acarinata* is a very fine-meshed species, it is quite difficult to observe the auxiliary opening in the side of the exserted vestibule on most specimens. Certainly the type material is too poorly preserved to enable the description of such features.

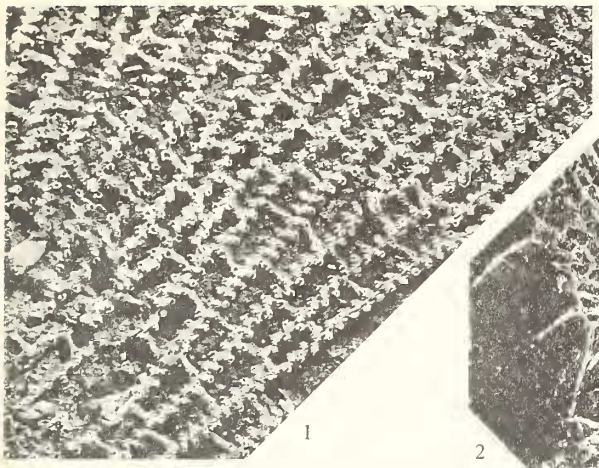
Stratigraphy. The species first appears in the *Schellwienella* cf. *burlingtonensis* Zone at Raglan (NUL448) and other stratigraphically similar localities. It is of common occurrence in the *Pustula gracilis* Zone at Rouchel Brook (NUL39) where the thin, zigzag branch form is most common. The species is plentiful in the *Orthotetes australis* Zone at Glen William (NUL361) and the type material comes from Hilldale (NUL372) which is situated low in the *Delepinea aspinosa* Zone. The final occurrence of the species is in the Barrington Guest House fauna (NUL414), a little higher in the above zone, where its range overlaps with the first occurrence of the two- to three-rowed species, *S. gloucesterensis* sp. nov.

EXPLANATION OF PLATE 70

All figures of latex casts except fig. 2.

Figs. 1–5. *Septatopora nodosa* sp. nov. 1, obverse surface of holotype exhibiting an ill-defined central carina, NUF2386, locality NUL258, × 10. 2, obverse mould of the base of a fan-shaped zoarium showing early branches bending away from the mesh to anchor the colony to the surface of a brachiopod, NUF2431a, locality NUL258, × 5. 3, reverse surface with spherical ovicells attached to the sides of the branches and projecting above the reverse surface level, NUF2525, locality NUL39, × 5. 4, obverse surface of NUF2524 illustrating strong development of a central carina in a low zonal form, locality NUL39, × 10. 5, obverse surface of NUF2523 showing multiple lateral branches developed from the side of a marginal branch in the positions normally occupied by dissepiments, locality NUL39, × 5.

Figs. 6–8. *Septatopora acarinata* (Crockford). 6, obverse surface of NUF2519 exhibiting large spherical ovicells positioned adjacent to the proximal rim of some apertures. Note also the zigzag obverse appearance of this low zonal form, locality NUL39, × 10. 7, obverse surface of a funnel-shaped zoarium, NUF2519, locality NUL39, × 5. 8, enlarged obverse surface of NUF2519 showing strong exsertion of septate apertures and the absence of a central carina and nodes, locality NUL39, × 20.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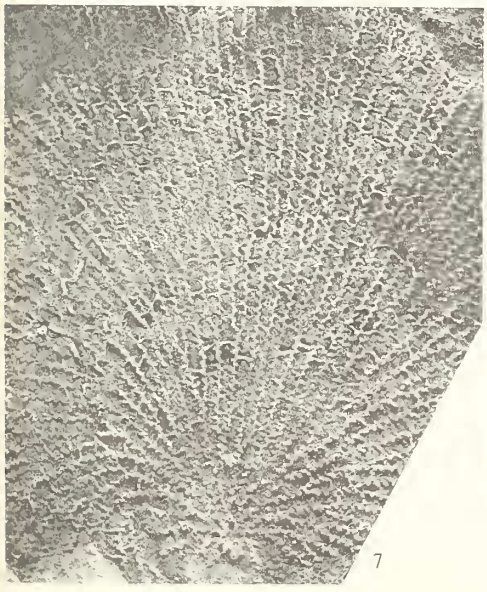
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8

ENGEL, *Septatopora*

Septatopora nodosa sp. nov.

Plate 70, figs. 1–5

Diagnosis. *Septatopora* with narrow, straight to zigzag, pustulose branches; mesh open, fine with sub-rectangular to rectangular fenestrules; apertures small, septate, closely spaced, strongly to moderately exserted with proximally associated hemispherical depressions and/or spherical bodies which project into fenestrules and on to reverse surface; zooecia in two rows per branch; carina weakly developed or absent; nodes small, closely spaced in a central row; reverse branch profile rounded, with spiny ornament; zooecial bases broadly triangular to pentagonal.

Description. *Zoarium*: radiating fan-shaped, gently undulose to laminate fragments of unknown orientation; some zoaria grow rapidly outwards in a fan shape from the base of the colony, in which specimens several of the outside branches droop away from the mesh to become recumbent sterile spine-like supporting anchors; maximum radius 50 mm. *Obverse surface.* (*a*) *Branches.* Straight or broadly curved, narrow (m.BW 0·25 mm); rounded with no carina or with low, indistinct median ridge between closely set nodes; profile strongly modified by apertural exsertion; ornament of fine, pustulose striations. (*b*) *Dissepiments.* Narrow (m.DW 0·09 mm); centrally straight with gradual expansion close to branch junction; slightly depressed below branch level; ornament of fine, pustulose striations. (*c*) *Fenestrules.* Sub-rectangular to rectangular; mesh fine, moderately regular, of even appearance; fenestrules short and narrow (m.FL 0·92 mm; m.FW 0·5 mm). (*d*) *Carina.* Lacking or represented by ill-defined ridge produced by narrowing of the branch profile; development variable within each zoarium. (*e*) *Nodes.* Small, erect, pointed nodes with rounded or slightly elongated bases; closely spaced (m.N–N 0·28 mm) with linear distribution in a central row; each node associated with an aperture on its disto-central rim. (*f*) *Zooecial apertures.* Small, circular (m.ZD 0·1 mm), strongly to moderately exserted; peristome narrow, raised, entire; apertures with eight septa surrounding a fine axial perforation; septa extend for only a very short distance down into the vestibule; erect apertures situated on branch shoulder and showing some slight lateral inclination; apertures indent fenestrule margin and may be stabilized with respect to the dissepiments on to which they frequently encroach; closely spaced (m.Z–Z 0·26 mm) with from three to five zooecia per fenestrule (m.Z/F 3·6); zooecia in two rows with a third appearing only in the fork at each bifurcation. (*g*) *Additional features.* A short horizontal tube proximally connects the upper exserted vestibule to the branch surface; ovicellular structures uncommon but when present they are usually located on the branch side in the fenestrule where they may also project around above the level of the reverse surface. Some specimens bear strong, ribbed, spine-like projections (diam. *c.* 0·2 mm) standing erect on the obverse surface at distant intervals.

Reverse surface. (*a*) *Form.* Branches and dissepiments rounded to slightly tapered with dissepiments at or below branch level; surface of branches and dissepiments longitudinally striate; high zonal specimens also bear numerous large pustules or small spines irregularly developed along the striations. (*b*) *Zooecial bases.* Broadly triangular; irregularly pentagonal on wider branches.

Material. Holotype NUF2386 (NUL258); paratypes NUF2388a/b, NUF2431a/b, NUF2445 (NUL258); NUF2523–2525 (NUL39); others NUF2432a/b, NUF2436–2438, NUF2385, NUF2387, NUF2389a/b, NUF2390–2391 (NUL258); NUF2404, NUF2424 (NUL414); NUF2488 (NUL448); NUF2522, NUF2526 (NUL39); NUF2412 (NUL361).

Remarks. The most distinctively different aspect of this species is its regular development of nodes. All other species of *Septatopora* either lack nodes or have them placed adjacent to some apertures in a generally irregular pattern. In *S. nodosa* they are associated with apertures but, because of the narrow branch width, they have assumed a linear, or slightly zigzag arrangement. In total appearance the species is not a good representative of the genus to which it has been attached with some misgivings. Were it not for the apertural septation, this species could be grouped readily with *Fenestella* Lonsdale.

The distinctively septate apertures and the proximo-lateral branch connection with an auxiliary tube form the basis of its assignment here to *Septatopora.* However, because of the short vestibular septa, mould infillings of the apertures do not always appear obviously septate and very close study is needed for correct generic assignment.

As in *S. acarinata* (Crockford), which shares a similar low zonal range with the present species, the oldest specimens have a very narrow branch profile which appears to zigzag between the exserted apertures. Subsequent material assumes a wider branch profile which eliminates this effect. Coupled with this, there is a reduction in the height of the low carina which becomes scarcely apparent, if at all.

A few specimens of *S. nodosa* have been found attached to the surface of brachiopods in the *Rhipidomella fortimuscula* Zone, where they use recumbent basal branches as an additional attachment device.

Comparisons. S. nodosa is the only species assigned to the new genus which can be reasonably compared with existing species of *Fenestella* Lonsdale. Generally, the distinction is readily based upon the development of apertural septation in *S. nodosa.*

Fenestella wilsoni Roberts occurs within a part of the range of *S. nodosa* and they share an identical mesh configuration. Because of a crystalline silica coating on all the type specimens of *F. wilsoni* it is difficult to observe apertural details, but it does not appear to be septate, and hence can probably be distinguished on this basis. Should better-preserved material of *F. wilsoni* be found, it may be possible to show that these two species are identical, but for the present they have been retained as separate taxa.

Other Lower Carboniferous species of *Fenestella* in Australia are readily distinguished on mesh grounds alone, quite apart from the apertural details.

Stratigraphy. S. nodosa first appears rarely in the *Schellwienella* cf. *burlingtonensis* Zone at Raglan (NUL448). It is of common occurrence in all subsequent zones up to and including the *Rhipidomella fortimuscula* Zone, thus spanning a range comparable with much of the Viséan interval.

Septatopora(?) *williamsensis* sp. nov.

Plate 68, figs. 1–3

Diagnosis. *Septatopora*-like species with straight, narrow, pustulose branches; mesh open, medium to fine, with sub-rectangular to rectangular fenestrules; apertures small, weakly septate, medium spaced being arranged on the extreme margin of the branch where only the fenestrular rim is weakly exserted; zooecia in two rows per branch; carina and nodes absent; reverse branch profile rounded; zooecial bases quadrate to pentagonal.

Description. *Zoarium*: small, radiating fragments of unknown orientation; maximum radius 20 mm. *Obverse surface.* (*a*) *Branches.* Straight to broadly curved, narrow (m.BW 0·22 mm); narrowly rounded without carina; ornament of fine, pustulose, longitudinal striations. (*b*) *Dissepiments.* Very narrow (m.DW 0·08 mm), centrally straight with moderate expansion at branch junction; situated well below branch level; ornament of longitudinal striations. (*c*) *Fenestrules.* Sub-rectangular to rectangular; regular mesh of medium size and open appearance; fenestrules of medium length, narrow width (m.FL 1·29 mm; m.FW 0·57 mm). (*d*) *Carina.* Absent. (*e*) *Nodes.* Absent. (*f*) *Zooecial apertures.* Small, circular (m.ZD 0·09 mm); weakly exserted with indistinct, low peristome developed only on the fenestrule margin of the aperture; apertures bear radiating septal plates which extend only half-way towards the axis and which do not extend far down into the vestibule; apertures situated low on the sides of the branch where they project weakly into the fenestrules with their low peristomal margin; inner apertural margins depressed into side of branch resulting in apertures which have a slight proximal and lateral inclination towards the fenestrule; moderately stabilized with respect to the dissepiments; zooecia medium spaced (m.Z–Z 0·32 mm) with from three to five zooecia per fenestrule (m.Z/F 4·0); apertures in two rows with a third row developing in the fork at each bifurcation.

Reverse surface. (*a*) *Form.* Rounded branches joined by narrower level dissepiments; ornament of fine, pustulose striations, identical to those of the obverse surface. (*b*) *Zooecial bases.* Quadrate to pentagonal in form being arranged in weakly overlapping rows.

Material. Holotype NUF2423 (NUL414); paratypes NUF2421–2422 (NUL414).

Remarks. The generic status of this species is somewhat doubtful. On the basis of its partly septate apertures and distinctive branch ornament it has been placed here with *Septatopora*. However, the lack of strongly exserted apertures and the absence of any auxiliary tube means that it lacks some of the essential diagnostic features of that genus.

As a relative of *Septatopora*, it would appear that the recessed apertures and short radial septa of this species produced only a partial constriction of the vestibule. This would mean it was still possible to extend both tentacles and lophophore perhaps making the development of an auxiliary tube unnecessary. The stratigraphic occurrence of *S.*(?) *williamsensis*, which correlates approximately with Mid-Viséan precludes any suggestion of an evolving sequence, since other species of *Septatopora* with

strongly developed apertural exsertion and septation are known from late Tournaisian onwards.

As it is outside the morphological limits of *Septatopora*, this new species really deserves its own generic category. However, until much more material of comparable form is found, it is not considered appropriate to propose such a taxon.

Another notable morphological aspect of *S.*(?) *williamsensis* is the wide expanse of central, obverse branch surface which lacks carina, nodes, and apertures. Indeed, both reverse and obverse surfaces are so similar that careful inspection of the apertural form is necessary to determine which surface is being examined.

No existing species of *Septatopora* or *Fenestella* in the Australian Carboniferous resemble this distinctive species.

Stratigraphy. *S.*(?) *williamsensis* has been found only at the Barrington Guest House locality (NUL414) where it is associated with *S. nodosa*, *S. acarinata*, and *S. gloucesterensis*. On the basis of the whole brachiopod-bryozoan fauna, this horizon has been placed in the lower parts of the *Delepinea aspinosa* Zone which correlates approximately with a Mid-Viséan age.

COMPARISON OF SPECIES OF *SEPTATOPORA*

Descriptive and statistical aspects of all nine species of *Septatopora* have been given in Tables 1 and 2.

From a study of information so displayed it is possible to indicate the general nature of variation present within the genus. Features which show very little variation include: (1) A standard zoarial form with only slight changes in fenestrule outline (oval to sub-rectangular). (2) A lack of any central carina on the branches (excluding *S. nodosa* sp. nov.). (3) Development of surface ornament in the form of distinctive pustulose striations. (4) Apertural septation. (5) Strong apertural exsertion with a high peristome forming a calice-like depression on each aperture. (6) Common surface development of hemispherical depressions proximal to some apertures in each zoarium.

By contrast the following features display considerable variation: (1) Increase in mesh size. (2) Increase in the number of zooecial rows per branch. (3) Increase in branch width and changes in branch profile. (4) Irregular nodal development. (5) Increase in apertural size and spacing. (6) Change in zooecial chamber form and auxiliary tube. (7) Variations in reverse surface ornament. Each of these aspects is detailed below with reference to the appropriate species and to the interval over which they have maximum zonal potential.

1. *Increase in mesh size*. Mesh dimensions reveal a progressive increase from small- to medium-sized species. Low zonal forms (*S. acarinata*, *S. nodosa*) are rather delicate compared with the larger species found in the high zones. Mesh variation is indicated by the large changes in fenestrule dimensions, shown in Table 2.

2. *Zooecial rows per branch*. A general trend throughout the Carboniferous in Australia is for all species of *Septatopora* to increase the number of zooecial rows per branch from two to four.

Low zonal species (*S. acarinata*, *S. nodosa*) are basically composed of two rows

TABLE 1. A descriptive comparison of the important morphological features of the fenestrate mesh of all species of *Septatopora*.

	Mesh	Branch Width; Form Profile	Fenestrules	Nodes	Apertural Size & Spacing	Zooecial Rows: Post bif. / Norm -al / Pre bif.	Zooecia per Fenestrule	Zooecial Bases	Branch Reverse
S. acarinata	fine, open	narrow; straight or zig-zag; narrowly rounded	sub-oval to sub-rectangular; short; narrow	-	small; close	2 / 2 / 3	3 - 4	irregularly pentagonal	rounded
S. nodosa	fine; open	narrow; straight to zig-zag; rounded	sub-rectangular to rectangular; short; narrow	close; central row	small; close	2 / 2 / 3	3 - 4	broadly triangular to pentagonal	rounded; spiny
S.(?) williamsensis	medium; open	narrow; straight; narrowly rounded	sub-rectangular to rectangular; medium length; narrow	-	small; medium	2 / 2 / 3	3 - 5	quadrate to pentagonal	rounded
S. gloucesterensis	fine; open	narrow to medium; straight; rounded	sub-oval to sub-rectangular; medium to short; narrow	medium spacing	small; close	2 / 2-3 / 4	4 - 5	irregularly pentagonal and rhomboidal	rounded
S.(?) sulcifera	medium; open	medium to wide; straight; oval	oval to sub-rectangular; medium length; medium width	-	small; close	2-3 / 3 / 3-5	(3)5 - 6	?	rounded
S. stellaris	medium to fine; even	medium; straight; rounded	oval to sub-oval; medium to short; medium width	distant spacing	medium; medium	2 / 2-3 / 3	2 - 3	(?) oval	tapered; spiny
S. isaacsensis	medium to fine; closed	wide; straight; oval	oval to sub-oval; medium to short; medium width	distant spacing	medium; medium	3 / 3 / 4-5	2 - 3	oval; no overlap between rows	tapered; spiny
S. pustulosa	medium; open	wide; straight; round-oval	sub-oval to sub-rectangular; medium length; medium width	-	medium; distant	2 / 3 / 4-5	3 - 5	elongate oval; no overlap between rows	rounded
S. flemingi	medium; closed	wide to very wide; straight; oval	sub-oval to sub-rectangular; medium length; medium width	-	medium; distant	2-3/3-4/5-6	3 - 5	elongate oval; no overlap between rows	rounded

per branch with additional apertures appearing only at bifurcation. *S. gloucesterensis* in the *Delepinea aspinosa* and *Rhipidomella fortimuscula* Zones has about equal development of two and three rows of zooecia between successive bifurcations. In the *Levipustula levis* Zone, *S. stellaris* continues in the trend of *S. gloucesterensis* but it is associated with *S. pustulosa* and *S. isaacsensis* which are dominantly three-rowed

TABLE 2. A statistical summary of the principal mesh dimensions of all species of *Septatopora*. Species known by only one specimen have only the mean and observed range recorded. Explanation of the abbreviations are given in the text.

		FL	FW	BW	DW	ZD	Z-Z	N-N	Nº	F/10	B/10	Z/5	Z/F
		mm	mm	mm	mm	mm	mm	mm					
S. acarinata	m	0·748	0·484	0·213	0·106	0·078	0·246	–	140	13·8	20·7	20·4	3·0
	s	*0·123*	*0·068*	*0·026*	*0·037*	*0·011*	*0·024*						
	OR	0·44-1·08	0·34-0·64	0·16-0·28	0·06-0·18	0·06-0·10	0·20-0·32						
S. nadasa	m	0·912	0·504	0·244	0·092	0·095	0·258	0·281	360	11·1	20·0	19·4	3·5
	s	*0·150*	*0·073*	*0·044*	*0·019*	*0·011*	*0·024*	*0·040*					
	OR	0·56-1·46	0·34-0·70	0·14-0·36	0·04-0·14	0·06-0·12	0·20-0·34	0·18-0·38					
S.(?) williamsensis	m	1·289	0·574	0·223	0·075	0·087	0·319	–	60	7·8	17·4	15·7	4·0
	s	*0·234*	*0·079*	*0·017*	*0·014*	*0·010*	*0·020*						
	OR	0·86-1·84	0·40-0·72	0·18-0·26	0·04-0·10	0·08-0·10	0·28-0·38						
S. gloucesterensis	m	1·116	0·581	0·297	0·183	0·098	0·272	0·512	40	9·0	17·3	18·4	4·1
	s	*0·080*	*0·106*	*0·030*	*0·027*	*0·009*	*0·019*	*0·089*					
	OR	0·96-1·28	0·44-0·86	0·24-0·36	0·14-0·26	0·08-0·12	0·22-0·30	0·34-0·64					
S.(?) sulcifera	m	1·358	0·742	0·411	0·200	0·069	0·288	–	20	7·4	13·5	17·4	4·7
	OR	0·76-2·24	0·70-0·76	0·35-0·50	0·14-0·22	0·04-0·08	0·24-0·32						
S. stellaris	m	0·953	0·633	0·361	0·140	0·128	0·333	0·951	40	10·5	15·8	15·0	2·9
	s	*0·079*	*0·092*	*0·053*	*0·029*	*0·013*	*0·031*	*0·150*					
	OR	0·70-1·10	0·50-0·86	0·28-0·46	0·10-0·24	0·10-0·16	0·28-0·42	0·60-1·22					
S. isaacsensis	m	0·914	0·747	0·470	0·263	0·120	0·324	0·937	20	10·9	13·4	15·4	2·8
	OR	0·82-1·00	0·60-0·96	0·34-0·60	0·18-0·40	0·10-0·16	0·26-0·38	0·70-1·20					
S. pustulasa	m	1·684	1·030	0·491	0·212	0·106	0·433	–	200	6·1	9·8	11·6	3·9
	s	*0·305*	*0·192*	*0·092*	*0·039*	*0·012*	*0·055*						
	OR	1·00-2·60	0·60-1·50	0·32-0·74	0·14-0·36	0·08-0·14	0·30-0·60						
S. flemingi	m	1·652	0·905	0·541	0·300	0·128	0·381	–	140	6·1	11·0	13·1	4·3
	s	*0·148*	*0·158*	*0·097*	*0·065*	*0·015*	*0·043*						
	OR	1·20-2·12	0·60-1·40	0·36-0·86	0·16-0·46	0·10-0·16	0·28-0·50						

species. Finally, in the *Cancrinella levis* Zone *S. pustulosa* is joined by *S. flemingi* which is dominantly four-rowed with pre-bifurcation increase up to five (rarely six) rows.

Both increase in mesh size and number of rows of apertures are universal trends which affect all Australian Carboniferous fenestrates. Increase is progressive in both cases and is not readily divided into arbitrary sub-groups.

3. *Branch width and profile.* Extra rows of zooecia, up to three rows, are accommodated in increasingly wider branches. Increase to four rows as in *S. flemingi* is, however, achieved by change in chamber arrangement which enables the extra row to be contained in branches which have not greatly increased in width.

Increase in branch width is also accompanied by a reduction in relative size of the fenestrule openings resulting in open-meshed forms changing to a closed-mesh appearance.

Variation in branch profile is considerable. As noted previously zigzag profiles of the low zonal species (*S. acarinata*, *S. nodosa*) change to a rounded profile in the *Orthotetes australis* Zone beyond which the profile gradually becomes more oval in form.

4. *Nodal development*. Some species of *Septatopora* lack any obverse nodes whereas others have irregular nodes adjacent to the distal or disto-central rim of some apertures. There appears to be no stratigraphic control over this feature which has resulted in three species groups.

(*a*) Nodeless: *S. acarinata*, *S.*(?) *williamsensis*, *S.*(?) *sulcifera*, *S. pustulosa*, *S. flemingi*.
(*b*) Irregular nodes: *S. gloucesterensis*, *S. stellaris*, *S. isaacsensis*.
(*c*) Regular nodes: *S. nodosa*.

No major importance above the species level can be given to the position and occurrence of these nodes. The absence of thin-section detail makes it unlikely that further functional significance will become known, and without this it is not possible to assess the weighting which should be given to this morphological feature. Even within node-bearing species some branches can be found which lack nodal development.

It is of some interest to note that most Australian species referrable to *Polypora* M'Coy also bear similar, randomly distributed nodes which differ in position from those of *Septatopora*, being placed adjacent to the proximal or proximo-central rim of an aperture rather than in the equivalent distal position.

5. *Increase in apertural size and spacing*. Low zonal species have slightly smaller apertures (mean range 0·07–0·1 mm) compared with the medium-sized apertures (mean range 0·11–0·13 mm) in the higher zones. In parallel with this variation the apertures change from closely spaced (mean range 0·25–0·29 mm) to distantly spaced (mean range 0·33–0·44 mm) over the same stratigraphic interval.

6. *Zooecial chambers and associated structures*. Chambers in two- or two to three-rowed species are globular in form and almost entirely fill the thickness of the branch. This form results in a very short vestibule beginning quite close to the obverse surface and extending up into the exserted aperture. In this case the auxiliary tube is only a breach in the side of the vestibule or a very short horizontal connection to the branch surface on the proximal side of the aperture. As such it is quite difficult to observe. With zigzag packing of globular chambers, the zooecial base form is irregularly pentagonal with considerable overlap between rows. Central rows of apertures appear rhomboidal in shape between the lateral rows.

With increase in the number of rows of apertures in the high zonal species (*S. pustulosa*, *S. isaacsensis*, *S. flemingi*), the chambers are necessarily packed much closer. They therefore assume an elongate, compressed-oval form with little or no overlap between rows. In addition, the flatter chambers are now located close to the reverse surface of the branch and this requires considerable changes in the shape of the vestibule. It is lengthened into an L-shaped or geniculate form with the auxiliary tube being connected to the short, posterior, horizontal section and extending up to the obverse surface in parallel with the longer anterior section of the vestibule. As

two quite separated structures they are now clearly visible on the obverse surface in their respective positions.

Primarily as a result of changes in branch width, the larger hemispherical depressions can also vary their position. On wide branches in the higher zones the branch width and zooecial spacing are sufficient to allow full development on the obverse branch surface. However, in the low zonal species the branch width tends to be very narrow and the apertures quite close together so that the spherical (?)ovicells are attached more to the side of the branch where they protrude into the fenestrules, or they can even continue around on to the reverse side of the zoarium where they may extend above the reverse surface level.

7. *Reverse ornament.* All except two species of *Septatopora* have a broadly rounded branch profile, joined by narrower dissepiments on the reverse surface. Normal ornament consists of distinctive pustulose striations similar to that developed on the obverse surface.

By contrast, two closely related high zonal species, *S. stellaris* (Campbell) and *S. isaacsensis* (Campbell) have a narrow, tapered reverse branch profile. Branches are joined by equal width, level dissepiments in a distinctive regular or proximally-polygonal mesh. The branches also bear a near central, very irregular array of numerous spines which are inclined distally.

Some features of reverse ornament are probably the product of exceptionally good preservation or are of some ecological significance. For example, all fenestrate genera from one locality (NUL258, Barrington, N.S.W.) have the same network of very fine spines or large thorny pustules over their reverse surface. This particular form of ornament has not been observed at any other locality.

AUSTRALIAN STRATIGRAPHIC DISTRIBUTION OF *SEPTATOPORA*

From the foregoing discussion, it is apparent that variation in the species of *Septatopora* makes it a most useful local zonal indicator. Text-fig. 2 sets out the range of all nine species in terms of the brachiopod zones of Campbell and McKellar (1969), Roberts and Oversby (1972), and Jones, Campbell and Roberts (1973) with which there is a strong parallel.

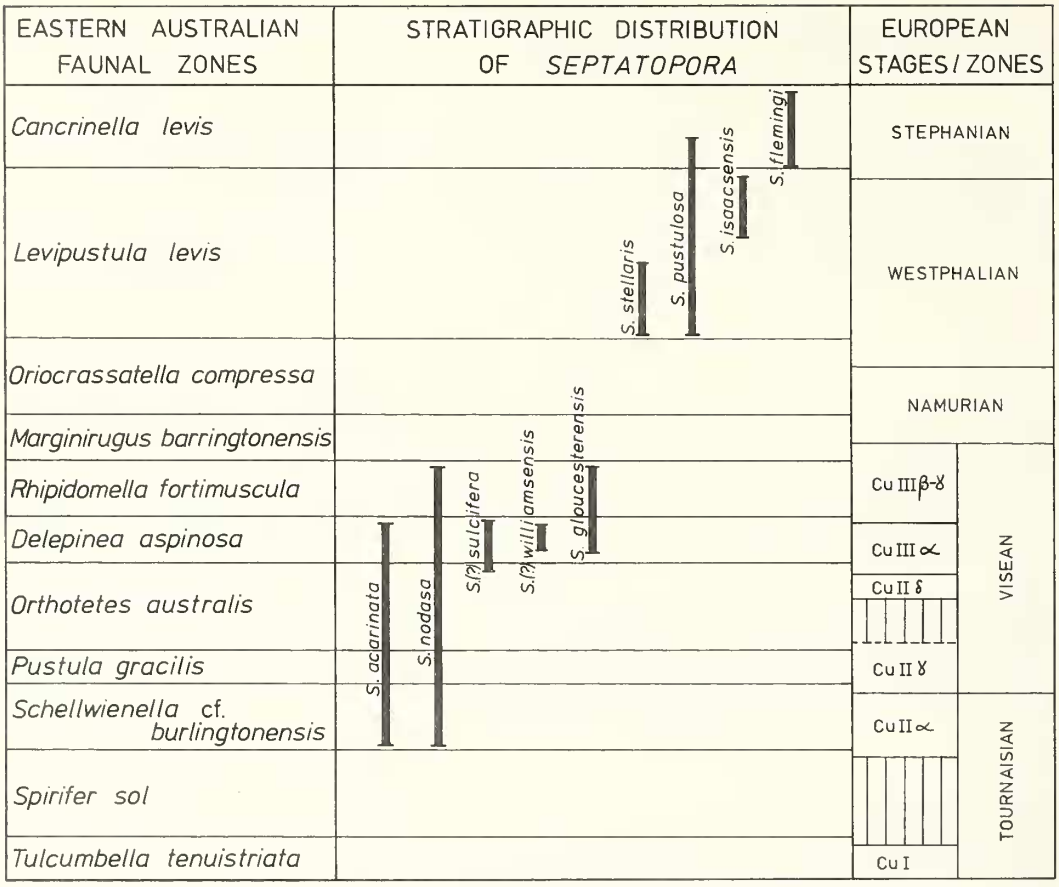
Tournaisian–earliest Viséan

Tulcumbella tenuistriata and *Spirifer sol* Zones have not yielded species referrable to the new genus. However, outcrops are few, and as other fenestrates are known from this level, it is quite possible that representatives will be found.

Schellwienella cf. *burlingtonensis* and *Pustula gracilis* Zones contain the first representatives of the new genus, namely *Septatopora acarinata* and *S. nodosa.* At this stratigraphic level, examples of both species have very narrow branches which zigzag between alternating apertures in a most distinctive pattern.

Viséan

Orthotetes australis Zone contains the same two species, but at this higher level both have developed wider, straight branches in which the apertures no longer are the dominating element.



TEXT-FIG. 2. Stratigraphic distribution of the various species of *Septatopora* in terms of the Eastern Australian Carboniferous zones. Tentative correlation with equivalent European zonation is also included.

Delepinea aspinosa Zone contains representatives of the two previous species plus *S.*(?) *williamsensis*, and the first of the two- to three-rowed forms *S. gloucesterensis* and *S.*(?) *sulcifera*.

Rhipidomella fortimuscula Zone contains *S. gloucesterensis* and *S. nodosa* with all other prior species having disappeared.

Late Viséan–Namurian–earliest Westphalian

Marginirugus barringtonensis Zone is dominated lithologically by coarse detrital sedimentary units within which no bryozoan remains have been preserved. Most brachiopods occur as reworked detrital shell deposits indicating a medium quite unsuited to delicate bryozoan preservation. The same observations are true for the *Oriocrassatella compressa* Zone (new) where large banks of heavy bivalve shells dominate the fossil record.

Westphalian–Stephanian

Levipustula levis Zone includes no species of *Septatopora* from lower stratigraphic

levels, although some generalized species of *Fenestella* (e.g. *F. osbornei* Crockford) do appear to have continued across the coarse sedimentary interval noted above. The fauna in this zone consists of *S. stellaris* (two to three rows), *S. pustulosa* (three rows), and *S. isaacsensis* (three rows) of which the three-rowed species are by far the most abundant forms.

Cancrinella levis Zone (new) includes the final species *S. flemingi* (three to four rows) together with *S. pustulosa*. The new species *S. flemingi* is the most common bryozoan at this level in a zone which is known only from regions of Carboniferous outcrop in east-central Queensland. The type locality for this newly defined zone is placed in the Stanwell–Ridgelands district where Fleming (1969) has published a geological map together with a description of some of the other elements of this late Carboniferous fauna.

It appears that *Septatopora* did not continue into overlying strata, for a literature survey of Australian Permian species referred to *Fenestella* Lonsdale and *Polypora* M'Coy has failed to reveal any probable members of the new genus. It is possible, however, that apertural septation has not been observed because of the generally poor state of preservation, in very coarse sandstones, of many Permian species. It should be noted also that the degree of apertural exsertion is slightly reduced in the final Carboniferous species, indicating that this may not be an obvious aspect in any Permian successors. Finally, it is of some value to indicate that most Australian Permian species of *Polypora* M'Coy have five or more rows of apertures, thus continuing the general trend noted in all Carboniferous fenestrates.

Correlation of the above assemblage zones with the European succession is difficult. Controls used by the previously mentioned authors in the definition of their Eastern Australian assemblage zones depend not upon the nominate, long-ranging brachiopod species, but upon the associated goniatites, a rare and often confusing component of the local faunas.

Initial correlation (Campbell and McKellar 1969) assumed that the standard German goniatite sequence was continuous. With the discovery by various European conodont workers including Rhodes *et al.* (1969, 1971) and Matthews (1969*a*, *b*, 1970*a*, *b*) that the Lower Carboniferous European goniatite sequence contains several major time gaps, the need arose to recorrelate the Eastern Australian zones. A definitive statement of the revised position is given by Jones *et al.* (1973) who give detailed arguments for their currently adopted position.

Assessment of the magnitude of the time breaks in the European sequence continues to present difficulties, making even the most recent efforts only very tentative. Conodont studies presently being undertaken by Dr. H. Jenkins and colleagues (University of Sydney) would suggest that the correlations adopted in text-fig. 2 must be revised so that the *Rhipidomella fortimuscula* Zone is of an early rather than late Viséan age, with the position of the Tournaisian–Viséan boundary remaining unaltered within the *Schellwienella* cf. *burlingtonensis* Zone. Changes of this magnitude in the Lower Carboniferous will obviously also vary the Upper Carboniferous correlations and hence it is not possible to offer confident comparisons at this stage. A study of the brachiopod content of the *Cancrinella levis* Zone reveals, however, a fauna of distinctively Permian affinities and it is with some confidence

that the range of *Septatopora* is extended up to the level of the late Westphalian or Stephanian age.

It is therefore concluded on present evidence that *Septatopora* ranges from late Tournaisian to Stephanian, at which point it appears to have become extinct.

GEOGRAPHICAL DISTRIBUTION

In Australia the pre-Carboniferous record is generally poor in fenestrates, so that no suitable ancestral material has yet been described.

With the possible exception of *Polypora*(?) *verrucosa* (M'Coy) no other described fenestrate has been observed in the literature, at present available to the author, which could be placed in *Septatopora*.

The only other record of the genus outside Australia would appear to be in the Upper Carboniferous of Argentina, where Amos and Sabattini (1969) and Mrs. N. Sabattini (pers. comm.) have listed the occurrence of several fenestrate species, originally described by Campbell (1961), some of which have been transferred here to the genus *Septatopora*.

Dependent upon further published descriptive details by Mrs. N. Sabattini, it would appear that *Septatopora* is another of the many genera shared in common by these two continents during Upper Carboniferous times.

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Finally, thanks are recorded for the support given by Mrs. N. Morris and a number of honours students at the University of Newcastle, whose field studies have allowed me to gather together a very large quantity of bryozoan material in the University of Newcastle collections.

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Addendum: The author has very recently been shown fenestrate specimens from the Middle Permian of the Bowen Basin, Queensland, which have strongly exserted apertures bearing eight apertural septa. This discovery thus extends the probable range of *Septatopora* gen. nov. into Permian strata in Eastern Australia.

As an oversight during manuscript preparation, reference has not been made to *Polypora stenostoma* Tavener-Smith (1971) which shares some aspects of morphological similarity with the new genus.

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